# VERTICAL DISTRIBUTION AND DIEL MIGRATION OF EUPHAUSIIDS IN THE CENTRAL REGION OF THE CALIFORNIA CURRENT

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## ABSTRACT

The density, vertical range, and diel movement of total zooplankton and euphausiid populations in the central region of the California Current were determined during a period of coastal upwelling, July-August 1970. Collections were made along four transects with opening-closing Bongo nets towed through 50- to 100-m intervals in the upper 800 m. Four- to nine-depth intervals at 13 day-night stations were sampled. Twenty euphausiid species from seven genera were identified from 124 hauls.

Zooplankton assemblages in the nearshore regions differed from those farther offshore in having a larger biomass as well as a smaller number and higher density of several species. Diel vertical movement among euphausiid populations, particularly *Euphausia pacifica*, tended to be more pronounced in offshore waters. This behavior suggests that, although assemblages of zooplankton are strongly structured by physical factors, some species alter their vertical distribution and diel migration, presumably in response to the prevailing food supply.

Since 1949 an intensive plankton sampling program has been conducted in the California Current under the auspices of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). These surveys, concentrating on the distribution and density of pelagic organisms in the upper 150 m, have revealed abundance and dispersion patterns of zooplankton which are related to annual and seasonal changes in hydrographic conditions (Brinton 1960, 1962a; Thrailkill 1963; Fleminger 1964, 1967; Alvariño 1965; McGowan 1967; Berner 1967; Isaacs et al. 1969). Within a given year, varying proportions of zooplankton assemblages typical of any one of several water masses are likely to be present (Berner 1957; Bieri 1959; Brinton 1962b; Johnson and Brinton 1963; Cushing 1971). Seasonal hydrographic fluctuations near the coastal boundary of the current act to further transform the numbers and types of pelagic species that develop. For example, the eutrophic environment produced by coastal upwelling during the spring and summer months is characterized by a much higher biomass and lower species diversity than the more oligotrophic, offshore portion of the current (Frolander 1962; Hebard 1966; Laurs 1967; Longhurst 1967; Pieper 1967).

Considerably less attention has been given to the vertical distribution of zooplankton in this current principally because it is difficult, time consuming, and costly to repeatedly sample discrete depths. The scope of this study was to describe the vertical distribution and diel migration of zooplankton, particularly euphausiids, in nearshore and offshore oceanic regions of the central California Current during a period when coastal upwelling was well developed. The samples were collected in the summer of 1970 on two cruises, Stanford Oceanographic Expedition (SOE) cruise 22 and CalCOFI cruise 7008.

## DESCRIPTION OF THE ENVIRONMENT

The California Current is a blend of water masses (Subarctic, North Pacific Drift, Central, and Equatorial) and is therefore an extremely variable environment (Reid et al. 1958; McGowan 1971). It flows southward throughout the year with an average velocity of less than 0.5 knot. The boundaries of this transitional water are between lat. 48° and 23°N and extend to 700 km (long. 130°W) from the coast. Between depths of 200 and 400 m, a subsurface countercurrent flows northward at about 0.5 knot from Baja California to Cape Mendocino (Kin'dyushov 1970).

Near the coast, hydrographic fluctuations in this current have been separated into seasonal periods of divergence (upwelling), relaxation (oceanic), and convergence (downwelling) (Bolin and Abbott

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1963; Dodimead et al. 1963). From March to August, the force of the prevailing northerly winds and the earth's rotation cause the southerly flowing surface waters, within 100 km of the shore, to move away from the coast (Yoshida 1955). This displaced water is replaced by cooler, more saline, nutrient-rich water upwelled from deeper regions, providing favorable conditions for high rates of primary production. In the central part of this current, the upwelling period is considered to begin and end with the shifting of the 9°C isotherm above and below the 100-m level (Barham 1957).

The northerly winds subside from September to November and surface water temperatures increase, resulting in the formation of a strong thermocline in the upper 50 m. During this surface-warmed period, in the absence of upwelling, tongues of offshore, oceanic water of the California Current may reach the coast. Where this occurs there is probably considerable mixing of oceanic and neritic planktonic communities (e.g., see Longhurst 1967).

When southerly winds prevail, in the period from December to February, a northerly flowing, coastal countercurrent (Davidson Current) may develop. Surface water converges toward the coast and disrupts the stratification characteristic of the surface-warmed water period. Vertical eddy circulation results, promoting the overturn, mixing, and downwelling of warm, lower salinity, nutrient-poor surface waters. This mixed water period can be characterized by a temperature gradient of less than 1°C in the upper 50 m.

The environments sampled at the shoreward and seaward stations in the summer of 1970 differed in several ways. Physical and chemical features relating to phytoplankton studies during the SOE cruise are presented in Malone (1971). These and other hydrographic features in the upper 800 m at each station are tabulated and discussed in Youngbluth (1973). By way of summary, it was clear from the low temperatures and high salinities and the shoreward elevation of nitrate isopleths that upwelling conditions prevailed near the coast. Chlorophyll-*a* values in the upper 150 m decreased with increasing distances from shore, 2.1-0.5 mg/m$^3$. The photic zone was usually deeper at the seaward stations, ranging from 55 m in coastal regions to 105 m at the western edge of the transects. The depth of the thermocline was shallower nearshore and deeper offshore, ranging from 5 to 40 m, respectively. The largest temperature difference between the thermocline and 150 m was about 4°C. At depths below 150 m, temperatures differed by 2°C or less among stations.

Temperature-salinity (T-S) curves from each station were compared to two different schemes (Youngbluth 1973). First, the data, when plotted with T-S relationships that characterize the percent mixing between waters near the northern and southern limits of the California Current (Okutani and McGowan 1969), indicated that between 150 and 800 m 70-100% northern water was present. The small percentage of southern water was most noticeable at the intermediate and nearshore stations of the southern transect. Second, the data, when contrasted with T-S curves that distinguish water masses, revealed that samples below 250 m were collected in North Pacific Intermediate water.

## MATERIALS AND METHODS

Zooplankton samples were collected with opening-closing Bongo nets of 0.333-mm mesh and cod ends with 0.222-mm mesh (McGowan and Brown 1966). At nearly all stations, shallow and mid-water casts were made, within 3 h of midday and midnight at nearly the same location (Table 1). Shallow tows were taken with a single frame (SOE) or with four frames (CalCOFI) in the upper 150-200 m. Three (SOE) or four (CalCOFI) frames were used on mid-water hauls between 200 and 600

TABLE 1.—The date and position of Bongo net tows.

| Cruise | Date 1970 | Station | Position | |
|---|---|---|---|---|
| | | | Lat. N | Long. W |
| SOE 22 | 27 July<br>28 July | 9 | 37°09′ | 124°24′ |
| | 29 July<br>30 July | 16 | 37°15′ | 128°45′ |
| | 31 July<br>1 Aug. | 25 | 36°39′ | 130°53′ |
| | 3 Aug.<br>4 Aug. | 39 | 39°54′ | 129°58′ |
| | 5 Aug.<br>6 Aug. | 47 | 39°53′ | 127°48′ |
| | 7 Aug.<br>8 Aug. | 56 | 39°53′ | 125°48′ |
| | 16 Aug.<br>18 Aug. | 68 | 43°49′ | 125°49′ |
| | 19 Aug. | 74 | 43°55′ | 128°03′ |
| | 20 Aug. | 81 | 43°32′ | 129°58′ |
| CalCOFI 7008 | 27 Aug.<br>28 Aug. | 70.75 | 35°23′ | 123°27′ |
| | 20 Aug.<br>21 Aug. | 50.80 | 38°40′ | 126°21′ |
| | 18 Aug.<br>19 Aug. | 50.110 | 37°40′ | 128°33′ |
| | 16 Aug.<br>17 Aug. | 50.140 | 36°40′ | 130°44′ |

m. Depth intervals of about 100 m were sampled. A single frame (CalCOFI) was employed at depths from 600 to 800 m. The nets were hauled along a single oblique path (all CalCOFI and shallow SOE casts) or undulated obliquely through the depth intervals sampled (all mid-water SOE casts). Each point on the graphs representing these data is the middepth of the water column sampled.

The strata sampled were recorded with a Benthos depth-time device attached a few meters below the bottom frame. Vessel speed during the tows ranged between 2 and 2.5 knots (3.7 and 4.6 km/h) and was regulated to maintain a wire angle of approximately 50°. Mean volumes of 619 $m^3$ (SOE shallow tows), 957 $m^3$ (SOE mid-water tows), and 546 $m^3$ (all CalCOFI tows) were filtered. All data were standardized to a volume of 1,000 $m^3$, assuming 100% filtration efficiency. Clogging of net apertures was observed only in the uppermost nets at the nearshore stations on the CalCOFI cruise.

The samples were preserved in 5% Formalin[2] solution buffered to pH 7.6. All organisms longer than 2 cm were removed from the sample and wet weights were determined after draining the remaining portion on a 0.222-mm mesh screen and blotting it on absorbent paper for 20 min. Duplicate estimates varied by an average of 6%.

The larvae (furcilia), juveniles (postlarvae and immatures), and adults (sexually mature) of all euphausiid species were studied. All individuals of the less abundant species were identified and counted. The densities of the more numerous species were determined from subsamples made with a modified Folsom Plankton Splitter. The average number of specimens examined in the subsamples was about 300. Duplicate counts were compared with each other by calculating a Percent Similarity Index (Whittaker 1952).

If the index indicated at least 80% agreement between the first two replicates, no other counts were made. Occasionally a third count was necessary.

The taxonomy of adult euphausiids follows Boden et al. (1955). Identification of certain difficult groups, e.g., *Nematoscelis* spp., *Thysanoessa* spp., and all larvae were verified by E. Brinton, T. Antezana, and K. Gopalakrishnan at the Scripps Institution of Oceanography. When specimens lacked some of the usual key characters, general body form and eye size, shape, and color were used to distinguish the species.

## RESULTS

### Sampling Variability Between Cruises

Samples were collected along four transects. The stations ranged from 130 to 693 km off the coast (Figure 1). During the CalCOFI cruise, a smaller average volume of water was filtered by each net. Presumably this smaller volume could have introduced some bias by reducing species diversity and abundance estimates. Comparisons of the results from each cruise indicate that, except for three rarely caught species: 1) the number of euphausiid species collected was identical and 2) the order of species abundances was quite similar on each cruise. Biomass values of total zooplankton tended to be larger at the seaward stations during the CalCOFI cruise. This difference is most likely related to the greater number and narrower, vertical width of the tows taken during this cruise, and, to some extent, growth and development of each life stage as well

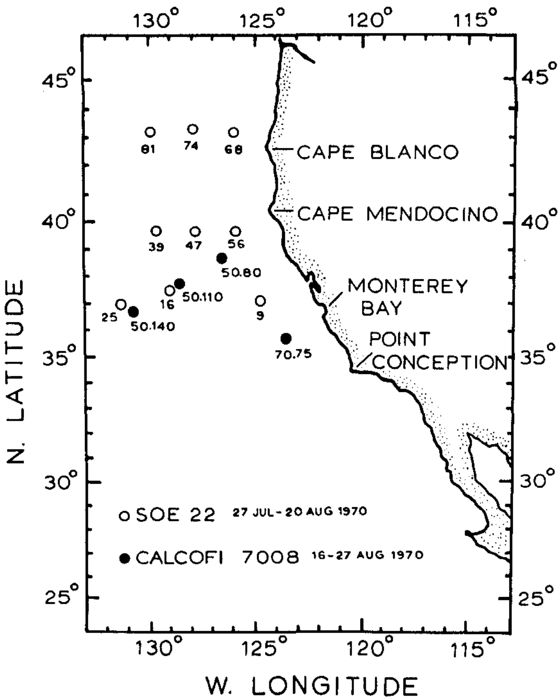


FIGURE 1.–Positions of the day-night stations in the central portion of the California Current.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

as offshore transport of the more numerous species observed in nearshore waters.

## Distribution of Zooplankton Biomass

The standing stock of zooplankton was highest at the nearshore stations and decreased with distances seaward. The largest and smallest biomass values occurred along the southern transect and corresponded with high and low phytoplankton stocks, respectively (Malone 1971).

Zooplankton were concentrated in the upper 100-150 m at most stations, particularly in the mixed layer (ca. 0-40 m). Densities ranged from 10 to 580 g wet wt/1,000 m$^3$ (Figure 2). Below 100-150 m, the amount of zooplankton at approximately 100-m intervals was generally between 25 and 150 g wet wt/1,000 m$^3$. Diel fluctuations in biomass were greatest in the surface water (0-150 m) increasing at night by factors of 1.2-8. At two nearshore stations, CalCOFI 50.80 and 70.75, large quantities of phytoplankton clogged net meshes in the upper 50 m and prevented any quantitative comparison of day and night catches. Below 150 m, a small but consistent increase in biomass was usually observed at night ($P$ = 0.20, Sign Test). During the day, at some intervals between 250 and 400 m, biomass was equal to or slightly greater than concentrations in the upper 150 m.

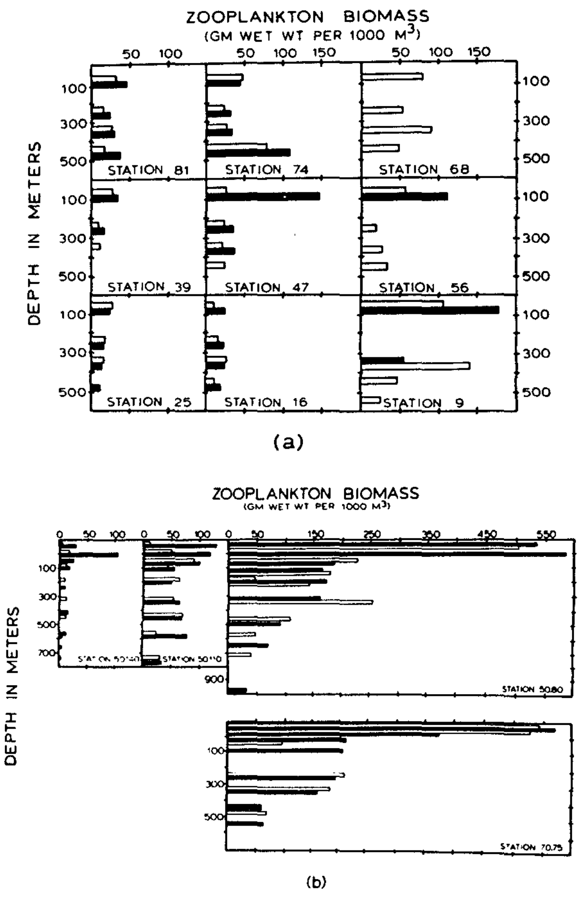


FIGURE 2.–The vertical distribution of zooplankton biomass. Clear bars indicate day samples; dark bars designate night samples. (a) SOE cruise 22 and (b) CalCOFI cruise 7008.

## Diversity, Density, and Distribution of Euphausiid Species

Twenty species of euphausiids distributed among seven genera were identified. Thirteen species occurred frequently enough and in sufficient numbers to allow descriptions of their vertical distribution. In the upper 150 m, 8 species formed 50% of the total abundance and 12 made up 90%. Nine species were found at more than half the stations. In the total water column sampled (ca. 0-700 m), 6 and 11 species composed 50 and 90% of the total species abundance. At most stations one or two species were numerically dominant.

The distributions of euphausiids at midday and midnight are discussed in the following paragraphs. Only examples of a few species are illustrated to represent the major patterns observed since a large number of profiles were derived from the data for all the species collected at each station (Youngbluth 1973). In many cases, diurnal changes in vertical distributions were obscured either by patchiness or avoidance or incomplete sampling due to gear failure or foul weather. This account is thus a composite description of the data from all stations.

### *Euphausia*

Four species of *Euphausia* were taken—*E. pacifica*, *E. recurva*, *E. gibboides*, and *E. mutica*. With the exception of *E. pacifica*, these species were only abundant at the offshore stations along the southern transects (SOE 16, 25; CalCOFI 50.110). In this region densities of each species usually ranged between 10 and 200/1,000 m$^3$. Juveniles and larvae were often more than twice as numerous as adults. The daytime habitat of *E. mutica* larvae was between 100 and 400 m. Juveniles of this species were found only in one haul which sampled from 400 to 500 m (SOE 16). *Euphausia gibboides* and *E. recurva* were collected somewhat deeper, 250-350 m and 400-600 m, respectively. At night all stages of these species migrated into the upper 100 m. *Euphausia mutica* and *E. recurva* appeared in the upper 50 m, whereas *E. gibboides* was more widely distributed with most of the population between 50 and 250 m (e.g., CalCOFI 50.140).

The relative abundance, vertical distribution, and diel migration of *E. pacifica* varied with distance from the coast (Figure 3). Data from all stations are illustrated to show the number of patterns exhibited by this species. Larvae and juveniles tended to occupy a much wider vertical range in nearshore waters. The bulk of the larvae was usually found in the upper 150 m day and night. The single exception to this pattern was observed at CalCOFI 70.75 where the larvae were abundant at 250 m throughout the day and in very large numbers in the upper 100 m at night. Juveniles were numerous in the surface waters as well as at depths to 450 m. The adult phase was frequently most abundant between 200 and 400 m during the daytime. Offshore, during the day, densities of this species were reduced, adults were rarely collected, and populations occurred at deeper, narrower intervals. At night, both nearshore and offshore, only some members of each stage migrated to the surface waters from depths of 250-450 m. The general features of the geographical distribution of this species in the central regions of the California Current agree with observations by Brinton (1962b, 1967); the vertical dimensions are more detailed.

### *Tessarabrachion*

The only species of this genus, *T. oculatus* was frequently found in small numbers, i.e., 10-20/1,000 $m^3$. Juveniles and adults of this characteristic subarctic species were common and occurred between 70 and 500 m. Somewhat greater numbers were collected at night. The larvae tended to remain closer to the surface, i.e., from 70 to 200 m (SOE 74; CalCOFI 50:110), than juveniles and adults which were usually found between 200 and 400 m. Thus, this species inhabits a wide depth interval below the thermocline regardless of the time of day.

### *Thysanopoda*

Three species of *Thysanopoda* were collected—*T. aequalis*, *T. acutifrons*, and *T. egregia*. Very few specimens of these species were taken. Larvae of *T. aequalis*, a species typical of central water masses, were found in the upper 200 m at the offshore stations of the southernmost transect. Adults, found only at night at the same stations, were collected above 300 m. Larvae of *T. acutifrons* were not observed. One juvenile and one adult were taken during the day between 400 and 500 m at different offshore stations. At night a total of 11 adults and 2 juveniles were caught between 200 and 500 m (SOE 16, 74; CalCOFI 50.110, 50.140). One to four larvae of *T. egregia* were collected between 50 and 450 m at nearly all but the most northern stations.

### *Thysanoessa*

Three species of *Thysanoessa* were found—*T. spinifera*, *T. gregaria*, and *T. longipes*. *Thysanoessa spinifera* was only collected near the coast, most frequently in the upper 150 m. Small densities of juveniles, the most abundant stage, were present in tows from 150 to 350 m (CalCOFI 50.80, 70.75). Adults were not collected. The preponderance of *T. spinifera* in the neritic environment has been noticed previously (Brinton 1962a; Hebard 1966). Diel changes in the vertical distribution of juveniles indicate that perhaps some members of this phase migrated into the upper 100 m at night (Figure 4a). These data support other studies that have suggested this species is a diel migrant (Regan 1968; Day 1971; Alton and Blackburn 1972).

*Thysanoessa gregaria* occurred at all but one location (SOE 68). This species was found most often in the upper 150 m, although it ranged to 300 m. Juvenile phases dominated the catches during the SOE cruise. All stages were abundant among the CalCOFI samples gathered 2 wk later. Densities were greater along the southern transects. From 50 to 500 individuals/1,000 $m^3$ were recorded within depth intervals where the largest concentrations occurred. Larvae usually resided in the upper 50 m. Juveniles and adults were numerous between 50 and 200 m and often 3-10 times more numerous in the night tows. These data suggest that the older stages probably avoided the sampling gear during the day. At one station (CalCOFI 70.75), all stages of *T. gregaria* were observed only in the upper 20 m during the day. At night this species ranged to 400 m with the largest densities occurring between 60 and 100 m and no specimens were collected in the upper 30 m. These

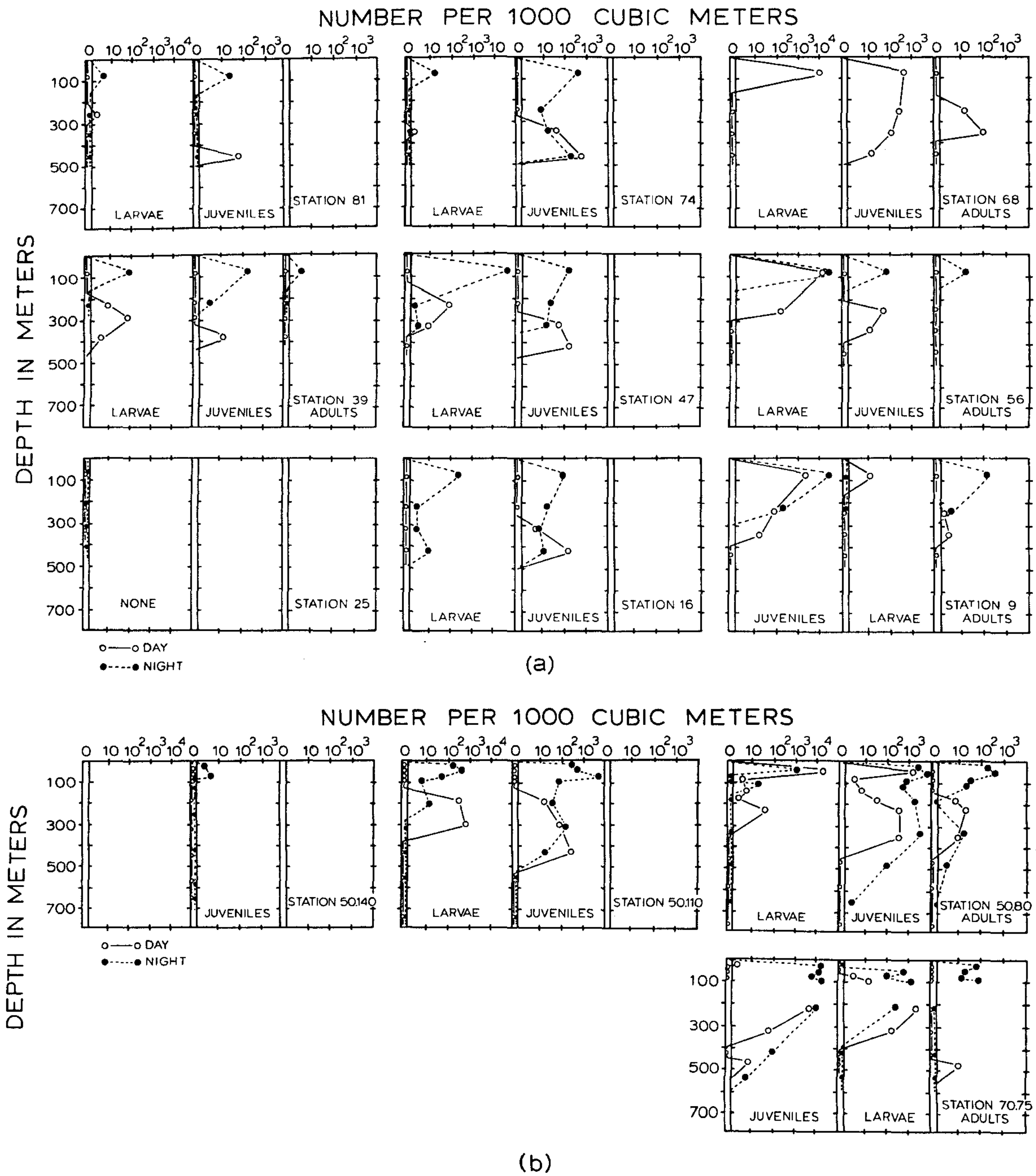


FIGURE 3.—The vertical distribution of *Euphausia pacifica* according to stage of development. (a) SOE cruise 22 and (b) CalCOFI cruise 7008.

observations indicate this species can be contagiously dispersed.

All phases of *T. longipes* (unspined form) were collected in the upper 150 m. Juveniles and adults were also abundant between 200 and 800 m. Portions of these older populations appeared to migrate toward the surface at night at several stations (SOE 9, 74, 81; CalCOFI 50.80, 50.110) (Figure 4b). The vertical range of this species agrees with observations by Brinton (1962b) and

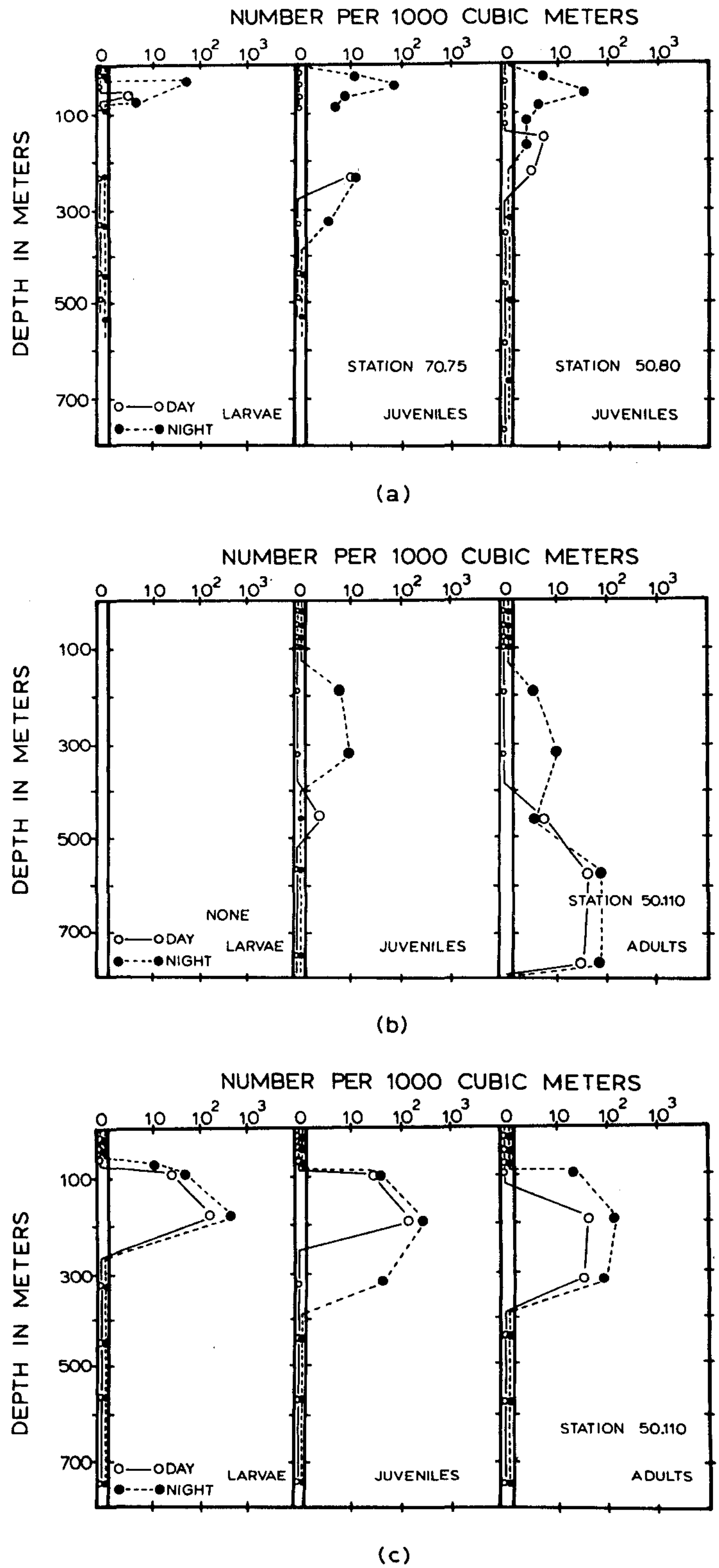


FIGURE 4.—Examples for the vertical distribution of (a) *Thysanoessa spinifera*, (b) *Thysanoessa longipes*, and (c) *Stylocheiron longicorne* according to stage of development.

Ponomareva (1963). The abundance in subsurface waters and the possible migratory behavior of this unspined form have not been documented previously.

### *Nematoscelis*

Two species of *Nematoscelis* were taken—*N. tenella* and *N. difficilis*. *Nematoscelis tenella* was collected at only one day-night station (SOE 16). The few adults and juveniles caught, 2-13/1,000 m$^3$, were found between 400 and 500 m during the day and 0 and 250 m at night. *Nematoscelis difficilis* occurred between the surface and 450 m at all but one station (SOE 25). This species was more abundant near the coast along the CalCOFI transect. Densities ranging in the hundreds per 1,000 m$^3$ at nearshore stations were an order of magnitude larger than concentrations among samples from waters farther offshore. Larvae and most juveniles were taken only in the upper 100 m. Adults were more abundant between 100 and 300 m, particularly at night.

### *Stylocheiron*

Five species of this genus were found—*S. affine*, *S. longicorne*, *S. maximum*, *S. elegatum*, and *S. abbreviatum*. These species occupied similar depth intervals day and night although each species tended to inhabit a separate portion of the water column. *Stylocheiron affine* occurred only along the southern transect. All stages were collected between 40 and 135 m and primarily at the most offshore stations where densities of 60-150/1,000 m$^3$ were recorded (SOE 25; CalCOFI 50.140). Each stage was often more abundant in the night samples. *Stylocheiron longicorne*, the most abundant species of this genus, ranged between 70 and 350 m, but the bulk of the populations were within the 150- to 250-m interval (Figure 4c). More specimens were usually caught at night. *Stylocheiron maximum* occurred in low densities at every station, i.e., 5-40/1,000 m$^3$. Larvae and juveniles of this species were found most often between 70 and 200 m. Adults were generally deeper, ranging from 200 to 400 m. Differences between day and night distributions indicate that this species migrated less than 100 m, if at all. Very small densities of *S. elongatum*, 1-27/1,000 m$^3$, were observed at the offshore stations between 200 and 600 m. A few adults of *S. abbreviatum* were found along the southern transect of the SOE cruise. Four individuals were collected in the upper 150 m at stations well offshore (SOE 25, 39) and one between 300 and 400 m nearshore (SOE 9).

### *Nematobrachion*

Two species of *Nematobrachion* were found—*N. boopis* and *N. flexipes*. One to two individuals of *N. boopis*, mostly juveniles, were taken between 300 and 500 m and only during the day at a few, southern stations (SOE 9; CalCOFI 70.75, 50.140). *Nematobrachion flexipes* occurred at all but one station (SOE 68). Small concentrations, usually 1-30/1,000 m$^3$ but ranging up to 69/1,000 m$^3$, were found regardless of the time of day. Juveniles were often the most numerous stage. This species was frequently encountered at 200-500 m during the day. At night specimens were collected from 450 m to the surface with most of a population in the upper 150 m.

## PATTERNS OF ABUNDANCE, VERTICAL DISTRIBUTION, AND DIEL MIGRATION

The abundance and vertical distribution of the more numerous euphausiid species in the upper 500-700 m differed in relation to distance from shore, longitudinal position in the area sampled, and vertical ranges occupied during a given day. The largest densities of euphausiids occurred near the coast (Table 2). Among the nearshore stations (ca. 100-150 km from the coast) *E. pacifica* was the numerically dominant euphausiid day and night, composing 75-90% of all species observed. At intermediate distances from the coast (ca. 300 km), *E. pacifica* was less abundant, making up 36-60% of the species collected, but still ranked first except in the north (SOE 74) where *Thysanoessa longipes* formed 69% of the day catch. Other euphausiid species constituting 15-30% of the total number included *S. longicorne*, *E. gibboides*, *T. gregaria*, and *T. longipes*. At stations farthest offshore (ca. 600-700 km) along the southern transects, *T. gregaria* and *S. longicorne* were the most abundant species, forming 75% of the total during the day. At night, larger numbers of *E. gibboides*, *E. mutica*, and *E. recurva* were collected such that these populations also ranked among 75% of the euphausiids collected. To the north, *T. longipes* and *S. longicorne* were the abundant species, composing 70-80% of all euphausiids. These changes in species composition and dominance represent the

TABLE 2.—The smallest and largest densities of all euphausiid phases among the depth intervals sampled. Data from night tows unless marked with a plus (+) sign which indicates densities are from day tows.

| | SOE transects | | | | | | | | | CalCOFI transect | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Northern stations | | | Central stations | | | Southern stations | | | | | | |
| Species | 81 | 74 | 68 | 39 | 47 | 56 | 25 | 16 | 9 | 50.140 | 50.110 | 50.80 | 70.75 |
| *Euphausia pacifica* | [1]27 | 9-540 | 72-10,783+ | 3-188 | 22-32,748 | 29,847 | — | 10-296 | 224-13,793 | 2-3 | 17-7,340 | 2-8,220 | 10-14,098 |
| *E. recurva* | 1 | — | — | 3 | 5+ | 1+ | 33 | 103 | — | 178-224 | 62 | — | 4+ |
| *E. gibboides* | — | — | — | 10 | 1-4+ | — | 198 | 9-207 | 2 | 2-82 | 6-26 | 2-9 | 4-24 |
| *E. mutica* | — | — | — | — | — | — | — | 7+ | — | 142-181 | 59-85 | — | — |
| *Tessarabrachion oculatus* | 1-3 | 11-31 | 2-34+ | 49 | 2-10 | 2 | 2+ | 1-11 | 9-54 | 2 | 2-16 | 5-20 | 2-8 |
| *Thysanopoda aequalis* | — | — | — | — | — | — | 4 | 7 | — | 4-44 | — | — | — |
| *T. acutifrons* | — | 1 | — | — | — | — | 1-2 | 1 | — | 2 | 2-2 | — | — |
| *T. egregia* | — | — | — | — | — | — | 4 | 2 | 1 | 3 | 2+ | 2 | 2+ |
| *Thysanoessa spinifera* | — | — | 14+ | — | — | 10 | — | — | 1-4 | — | — | 2-37 | 4-118 |
| *T. gregaria* | 25 | 2 | — | 33-34 | 81 | 29 | 1-173 | 3-71 | 6-142 | 4-646 | 2-481 | 3-223 | 7-768 |
| *T. longipes* | 8-109 | 27-197 | 4-134+ | 321 | 17-303 | 33 | — | 3 | 59-141 | 2 | 9-89 | 6-94 | 6-12 |
| *Nematoscelis tenella* | — | — | — | — | — | — | — | 3-4 | — | — | — | — | — |
| *N. difficilis* | 8 | 1-9 | 4-4+ | 9-9 | 2-7 | 3-3 | — | 33-43 | 89-109 | 15 | 8-26 | 8-512 | 12-189 |
| *Stylocheiron affine* | — | — | — | — | — | — | 62 | 1-18 | — | 2-151 | 2 | 6 | 11-18 |
| *S. longicorne* | 2-55 | 3-4 | 2+ | 34-52 | 2-53 | 11 | 1-295 | 17-73 | 26-229 | 8-130 | 2-900 | 2-248 | 4-68 |
| *S. maximum* | 1-5 | 2-2 | 1+ | 8 | 2-7 | 2 | 1-16 | 2-6 | 3-19 | 2-20 | 4-16 | 6-20 | 2-48 |
| *S. elongatum* | — | — | — | 1 | 1+ | — | — | 1-4 | — | — | — | — | — |
| *S. abbreviatum* | — | — | — | 2+ | — | — | — | — | 1+ | — | — | — | — |
| *Nematobrachion boopis* | — | — | — | — | — | — | — | — | 1+ | 2+ | — | — | 2-2+ |
| *N. flexipes* | 1-15 | 1-5 | — | 51 | 1-3 | 2 | 16 | 1-37 | 1-4 | 10-37 | 2-28 | 2-24 | 2-13 |
| Number of depth intervals sampled | 4 | 4 | 4 | 2 | 3 | 1 | 4 | 4 | 2 | 9 | 9 | 9 | 8 |

[1]A single density indicates a species was captured within only one depth interval.

complex interaction of: 1) the recruitment and mixing of species characteristic of the water masses that compose the California Current, 2) the daily vertical movements of euphausiids, 3) the ability of most species to avoid the sampling gear, and, to some extent, 4) their contagious dispersion. Consequently only the more obvious patterns have been noted.

The vertical distributions of adults and juveniles in the upper 500-700 m are summarized in Table 3 and compared with data from the southern part of the California Current. As previously mentioned, 7 of the 20 species collected appear to be diel migrants. Distances of 300 m or more were traversed by four species of *Euphausia*. Portions of other populations such as *Nematobrachion flexipes*, *T. longipes*, and *T. spinifera* may migrate up to 200 m.

The larval phases of most species live in the upper 150 m. *Tessarabrachion oculatus* and *Stylocheiron* spp. larvae were found more often below the thermocline. The young of *Euphausia* spp. tended to occupy and migrate through the same depths as the older stages. In nearly all instances, differences in density between day and night catches of larvae were small.

The nonmigrating species included *Thysanoessa gregaria*, *Tessarabrachion oculatus*, *S. maximum*, *S. affine*, and *S. longicorne*. The first three species were usually scattered throughout a broad vertical range. The other two species, *S. affine* and *S. longicorne*, were vertically segregated and occurred within much narrower depth intervals. The different strata occupied by these two nonmigrating species was also observed in other regions by Brinton (1967), Baker (1970), and Youngbluth (1975).

## DISCUSSION

Differences in the distribution patterns of many species of zooplankton have been associated with their response to environmental gradients, particularly temperature and illumination (Harris 1953; Lewis 1954; Banse 1964; Boden and Kampa 1967). In this study, the causative factors influencing vertical and horizontal distributions are difficult to elucidate. It is clear, however, that the thermocline was an upper distribution boundary for several species, e.g., *T. oculatus*, *E. gibboides*, *S. affine*, *S. longicorne*, and *S. maximum*. In the southern part of the California Current, the upper range of these species was also restricted by the thermocline (Brinton 1967). Studies on the tolerance of *E. pacifica* to changes in temperature and salinity suggest that other unknown factors probably regulate its distribution in the California Current (Gilfillan 1972a, b).

Recently Isaacs et al. (1974) have proposed that "by responding to light intensity, most vertically migrating marine creatures are directed to food. ... In areas of low standing crops of phytoplank-

TABLE 3.–Comparisons of diel changes in the vertical distributions of adult and juvenile euphausiids. Depth ranges (m) are 10% and 90% levels.

| Species | Central California Current | | Southern California Current (Brinton 1967) | |
|---|---|---|---|---|
| | Day | Night | Day | Night |
| *Euphausia pacifica* | 20-500 | 0-450 | 150-425 | 0-150 |
| *E. recurva* | 300-600 | 0-50 | 180-550 | 0-150 |
| *E. gibboides* | 300-600 | 10-150 | [1]300-500 | 40-120 |
| *E. mutica* | [2]370-470 | 0-150 | — | — |
| *Tessarabrachion oculatus* | 70-450 | 70-450 | — | — |
| *Thysanoessa spinifera* | 125-300 | 0-150 | — | — |
| *T. gregaria* | 0-200 | 0-350 | 20-180 | 0-250 |
| *T. longipes* | 0-800 | 0-800 | — | — |
| *Nematoscelis difficilis* | 0-400 | 0-400 | [2]50-200 | 0-275 |
| *Stylicheiron affine* | 40-100 | 35-100 | [3]50-200 | 15-250 |
| *S. longicorne* | 100-350 | 100-350 | 125-300 | 125-300 |
| *S. maximum* | 70-450 | 70-450 | [4]130-200 | [4]130-200 |
| *Nematobrachion flexipes* | 200-500 | 0-130 | 100-450 | 100-350 |
| Sampling range (m) | 0-800 | | 0-600 | |
| Sampling interval | 50-150 | | 25-100 | |
| Gear employed | Bongo nets | | Leavitt nets | |
| Mesh opening | 0.333 mm | | 0.550 mm | |

[1]Adults only.
[2]Based on seven specimens from one station.
[3]Mostly juveniles.
[4]Maximum concentration of juveniles.

ton, daylight penetrates further into the ocean causing the migrating animals to descend deeper. In the turbid water associated with high standing crop, the migrating forms remain closer to the surface." Observations on the vertical distribution and daily movements of one euphausiid species in this study lend support to this hypothesis. In more turbid, upwelled water near the coast where standing stocks of phytoplankton were greater (e.g., CalCOFI 50.80), populations of juvenile *E. pacifica* were larger and extended over wider vertical ranges but their diel vertical migrations were not pronounced. In clearer, more oligotrophic waters farther offshore (e.g., CalCOFI 50.110; SOE 16, 47, 74), populations were reduced in size, occupied deeper, usually narrower depth intervals, and daily vertical movements were more obvious. From these few observations it appears that density levels and migration intensities of this species may be coupled with the standing stock of phytoplankton in surface waters.

The persistence of nonmigrating forms, e.g., *Stylocheiron* spp., within the same, relatively narrow depths day and night in waters of varying origin and the recurrence of the finding in this and other studies (Brinton 1967; Youngbluth 1975) that only a portion of a population categorized as a migrating form, e.g., *Euphausia* spp., may actually make daily vertical movements to surface waters, suggest that factors in addition to temperature and light act to regulate the distributions recorded. These observations indicate that more attention should be directed toward sampling those horizons where zooplankton populations are concentrated to determine how distributional and behavioral patterns are structured by the physical and biological fluctuations within their preferred habitats.

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